

Zusammenfassung

Verhaltensphysiologische und elektroфизиologische Untersuchungen zur Riechfähigkeit von Albinomäusen

Bei ♂♂ Albinomäusen wurde die Riechleistung mit verhaltensphysiologischen und elektrophysiologischen Methoden untersucht. Die olfaktorischen Schwellen (Geraniol, Buttersäure) der drei Tiere, bei denen anschließend an eine Geruchsdressur Ableitungen vom Bulbus olfactorius durchgeführt wurden, lagen bei beiden Methoden im gleichen Größenordnungsbereich. Bei 24 weiteren Mäusen wurden neurale Schwellen mit Hilfe evozierter Potentiale sowie durch eine Frequenzanalyse der für den Bulbus olfactorius charakteristischen Oszillationen bestimmt. Die Übereinstimmung der in verhaltens- und elektrophysiologischen Experimenten ermittelten Ergebnisse rechtfertigt es, auch bei den neuronalen olfaktorischen Reaktionsschwellen von Riechschwellen zu sprechen.

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Habitat selection and fluctuations in numbers in a population of the arctic hare (*Lepus timidus*) on a subarctic fell in Finnish Forest Lapland

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Receipt of Ms. 20. 11. 1981

Abstract

Habitat selection and population fluctuations were studied in the arctic hare (*Lepus timidus*) in the Värriötunturi fell area, East Finnish Forest Lapland, in the winters of 1968/69–1980/81. A transect survey indicated that the density of the population fluctuated in cycles of at least four years. Only the preferred habitats (i.e. lowland conifer-dominated mixed forests with birch and/or characterized by juniper) were inhabited during a population low, while in peak winters hares also occurred in less favoured habitats (e.g. mountain birch forests on windy slopes). The population decline is not triggered by predation. The movement activity of the hares when searching for food may increase considerably in the late winter at times of high populations.

Introduction

Cyclic fluctuations and their causations in populations of the snowshoe hare (*Lepus americanus*) in the boreal forests of North America are relatively well known (see GREEN and EVANS 1940; KEITH 1963; KEITH and WINDBERG 1978; FINERTY 1980), whereas fluctuations in those of the arctic hare (*Lepus timidus*) in the boreal and subarctic forests of Fennoscandia are poorly documented (for data, see SIIVONEN 1948; HÖRNFELDT 1978). Very little is known even about habitat selection among arctic hares under conditions in which different fell zones are available, although the composition of the winter food of the species under such conditions is better known (see PULLIAINEN 1971, 1972; LINDLÖF et al. 1974a, b).

The present author began a census of hare tracks on a subarctic fell in eastern Finnish Forest Lapland in the winter of 1968/69 and results from 13 successive winters are now available. The purpose of the present paper is to provide records on habitat selection and fluctuations in numbers during these winters.

Study area

The study area lies in eastern Itäkaira, Finnish Forest Lapland. The area includes two fell ridges (Pulkkatunturi – Sautunturi and Värriötunturi) running in a north-south direction about 5 km apart. It is in a virgin state, with the following proportions of natural habitats in an area of approximately 200 km²: spruce forests (*Picea abies*) 26.5 %, Scots pine forests (*Pinus sylvestris*) 18.5 %, birch forests (*Betula* spp.) 3.0 %, mixed forests 22.0 %, open bogs 13.5 %, mountain birch forests (*Betula pubescens tortuosa*) 7.0 % and treeless fell summits 9.5 %. The forests are old and mature, including a large number of standing and fallen dead trunks. The density of the trees is generally very low, and in some places there are young spruce, pine and birch saplings growing among the very old trees. Some of the lowland birch forests were killed by larvae of the geometrid *Epirrita autumnata* in 1965–1966 (see PULLIAINEN 1976). The study area lies 266–475 m above sea level.

Methods

The numbers of arctic hare and mammal predator tracks crossing an observation line 5970 m long running westwards from the summit of Värriötunturi were recorded in the winters of 1968/69 to 1980/81 by skiing along this line once a week. Only tracks which were two days old or fresher when recorded in November–April (identified on the basis of the snowfall and wind data from the nearby meteorological screen and the states of freezing of the tracks) are taken into account in the present calculations. If the same individual had crossed the line in a zig-zag manner between two recording sticks 30 m apart, this was regarded as only one crossing.

Some months contained four recordings and some five, and in some cases a heavy snowfall had covered the fresh tracks of the mammals in question. All values representing each habitat type were first calculated per 100 m of the observation line, rendering the recordings made in different habitats comparable one with another. All monthly means were then standardized to four recordings. If a heavy snowfall or strong wind had recently covered the tracks, these cases were omitted, and the monthly means were calculated on the basis of those recordings from the month in question in which recent tracks were visible.

The observation line ran through the following habitats (distances covered in parentheses):

- (A) Almost treeless summit of the Värriötunturi fell (510 m).
- (B) Mountain birch forest on the western slope of Värriötunturi, were mountain birches (B) comprised a half of the trees, the other half consisting of pines (P; 20–40 %), spruces (S; 0–10 %) and junipers (J; *Juniperus communis*; 10–20 %) (570 m).
- (C) Spruce-dominated forest: S 40–85 %, P 0–40 %, B 5–30 % and J 0–10 % (1860 m).
- (D) Pine-dominated forest: P 70–80 %, S 0–10 %, B 5–10 % and J 10–15 % (1200 m).
- (E) Mixed forest characterized by juniper: J 55–75 %, S 5–15 %, P 0–20 % and B (living, since some had been destroyed by *Epirrita autumnata*) 10–20 % (1200 m).
- (F) A bog: willows (*Salix* spp.) 80 %, B 10 % and S 10 % (30 m).
- (G) A treeless marsh (600 m).

Table

Mean numbers of tracks (per 100 m of the observation line) of the arctic hare recorded crossing the observation line in different habitats (for descriptions, see text) and total numbers of these tracks (calculated per 4 recording times each month) in the winters of 1968/69–1980/81

Winter	Habitats						Total no. of tracks		
	C "spruce-dom. forest"	E "juniper-char. forest"	D "pine-dom. forest"	B mountain birch forest	F "willow bog"	A treeless summit	G open bog	Nov.–Febr.	Nov.–April
1968/69	0.37	0.43	0.32	0.32	—	0.20	0.12	75.0	111.4
1969/70	1.08	0.65	0.40	0.43	1.10	0.05	0.40	91.0	227.0
1970/71	0.57	0.67	0.43	0.35	—	0.65	0.07	115.8	174.8
1971/72	0.18	0.07	0.10	0.17	—	—	0.10	23.2	39.8
1972/73	0.34	0.55	0.18	—	—	0.03	0.02	69.6	94.0
1973/74	0.72	0.25	0.57	0.37	—	—	0.02	99.0	150.2
1974/75	0.50	0.75	0.68	0.12	—	0.18	0.05	136.8	170.4
1975/76	0.15	0.30	0.08	—	—	—	—	14.0	41.9
1976/77	0.43	0.45	0.13	0.10	—	—	0.10	73.8	93.8
1977/78	0.32	0.30	0.10	0.35	0.55	0.33	0.15	56.6	93.2
1978/79	1.08	0.57	0.82	0.60	0.55	0.35	0.23	125.0	260.0
1979/80	0.92	0.82	0.45	0.07	—	—	0.33	132.6	204.6
1980/81	0.92	1.13	0.77	0.17	—	0.20	0.13	198.1	257.1
Mean ± S.E.	0.58 ± 0.09	0.53 ± 0.08	0.39 ± 0.07	0.23 ± 0.05	0.17 ± 0.10	0.20 ± 0.06	0.13 ± 0.03		
Mean ± S.D.	± 0.33	± 0.28	± 0.26	± 0.18	± 0.35	± 0.20	± 0.12		
t-test	0.669	2.337	2.243	0.868	0.167	0.319			
		p < 0.05	p < 0.05						

Results

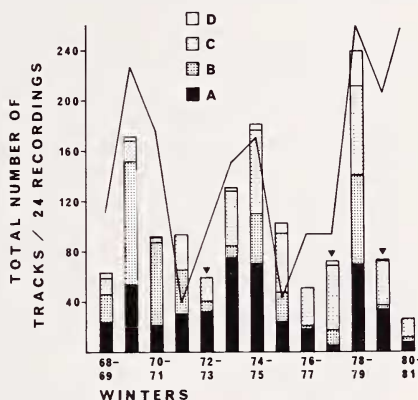
Habitat selection

The spruce-dominated and juniper-characterized mixed forests were clearly the most favoured habitats for the arctic hares (Table). The pine-dominated mixed forests formed an intermediate group. Arctic hares were recorded every winter in these three habitats, whereas they were absent from the rest of the habitats available in at least one winter, and the mean numbers of tracks were also smaller than in the first three habitats. In three winters (1969/70, 1977/78 and 1978/79) the arctic hares occurred in all the habitats studied, and in one winter (1975/76) they were found only in the three most favoured ones.

Fluctuations in numbers

Track counts during 13 winters indicated two lows, namely the winters of 1971/72 and 1975/76, and three peaks, the first in the winter of 1969/70, the second in 1974/75, and the third in 1978/79. Thus the two lows followed each other at an interval of four years, and the three peaks at intervals of five and four years. The timing of the third peak may be somewhat later, however, as this has now lasted three winters. The pattern stands out more clearly if the conclusions are made on the basis of the total numbers of tracks recorded in November-February in each winter (Table). Then the timing of the lows and the second

Total numbers of tracks of arctic hares (solid line) and small carnivores (columns: A = *Vulpes vulpes*, B = *Mustela erminea*, C = *Martes martes* and D = *Mustela nivalis*) recorded crossing the observation line during the winters of 1968/69-1980/81 (numbers calculated per 24 recording times). Triangles indicate the years in which *Aquila chrysaetos* nested in the nearby aerie



peak are the same, but the first peak is located one year later (in 1970/71) and the third two or more years later. The intervals between the two lows and between the first two peaks are then four years, and that between the second and third peak at least six years.

The reason why the two methods of calculation give partly different results is that the mean number of tracks per 100 m of the observation line in each of the most favoured habitats increased significantly in late winter in the peak winters, but not during the other winters.

Of the carnivores inhabiting the area studied here, the following can be regarded as potential predators upon young and/or adult arctic hares: the red fox (*Vulpes vulpes*; see SEQUEIRA 1980), the pine marten (*Martes martes*; PULLIAINEN 1981a), the stoat (*Mustela erminea*; ERLINGE 1979) and the pygmy weasel (*Mustela nivalis*; PULLIAINEN and IIVANAINEN 1979), together with the great predators, among which the wolf (*Canis lupus*; PULLIAINEN et al. 1980) and wolverine (*Gulo gulo*; PULLIAINEN 1978) are only occasional visitors to the area and the lynx (*Felis lynx*; PULLIAINEN 1978) a very rare visitor. Observations made at the nest of the local pair of Golden Eagle (*Aquila chrysaetos*) showed

that arctic hares are an important source of food for them, at least during the nestling period. The years in which the nearest pair hunting in the area also nested there are marked in the Fig. as also are the total numbers of tracks of the red fox, pine marten, stoat, pygmy weasel and arctic hare crossing the observation line during the winters concerned. The numbers of both the hare and the predator tracks were greatest in the winters of 1969/70, 1974/75 and 1978/79.

Discussion

Arctic/subarctic hares are regarded as typical floaters in their food intake in winter (see PRUITT 1970), although they may also occasionally dig out food items from under the snow (PULLIAINEN 1972). According to BRYANT and KUROPAT (1980), the forage preferences of snowshoe hares and arctic hares follow the pattern willow > aspen > larch > dwarf birch > tree birch > pine (including Scots pine) > fir > spruce > alder. Arctic hares eat the woody internodes of *Betula pubescens* and *Populus tremula*, but reject the foliar buds (BARIKMO 1976). Juvenile-growthform twigs in the browse material appear to be less palatable than the mature-growthform twigs of the same plant species (BRYANT 1980).

Since there are no larches and very few willows, aspens or dwarf birches available in the present area (PULLIAINEN 1971, 1972), it is understandable that about 65 % of the feeding observations made on arctic hares during two successive winters should have concerned the twigs, bark, catkins and decayed wood of birch, and the shoots and bark of juniper (PULLIAINEN 1972). When juniper was plentiful, its importance seemed to increase at the expense of birch. During snowy winters, however, the majority of the juniper bushes (and willows and dwarf birches) are covered by the snow.

Especially in the mountain birch forest zone of Värriötunturi, but also to some extent in the lowlands, accumulations of hoarfrost and snow on the tops of birches and other trees and bushes bend the tips of the branches and other parts to levels at which they can be reached by the hare (PULLIAINEN 1972). Taking this into account, together with the structure of the forest and the relatively high temperatures on the slopes of the fell as compared with the lowlands (see HELIMÄKI 1974), the mountain birch forests might have been expected to be the preferred habitats of the present arctic hares, but this was not the case (Table). Among the biotopes of southern Scandinavia studied by LINDLÖF et al. (1974a), clearings and pasture-land overgrown with birch, all of which had a rich undergrowth, were most utilized by hares, while mixed coniferous forests and open bogs were less favoured.

The arctic hares of this area clearly preferred the conifer-dominated and juniper-characterized mixed forests as their habitats (Table), although the conifers themselves are only exceptionally of nutritional importance for them, and then only in the form of fallen pine branches (see PULLIAINEN 1971, 1972). It may be that, on the one hand, the hares avoided the warm but windy slopes and summit of the fell (HELIMÄKI 1974), and on the other hand, they had found other acceptable food in addition to birches and junipers (e.g. grass and herbs, see PULLIAINEN 1972) and obtained shelter under the lower branches of the spruces and fallen trunks of the conifers. The prevailing low temperatures, often below -30°C due to temperature inversion, seem to be of little or no importance in the habitat selection of the local arctic hares.

The snowshoe hare populations of the North American boreal forests exhibit a long-term periodicity, mainly of 8 to 11 years (KEITH 1963), but not those in the southern part of the range (HOWELL 1923; LEOPOLD 1933; WOLFF 1977). In both areas increased hare densities lead to dispersal into less favourable habitats (KEITH 1974; DOLBEER and CLARK 1975; WOLFF 1977). Assuming that the changes in the total numbers of tracks crossing the present observation line per winter reflect corresponding changes in the density of the hare population, a similar trend can be said to be recorded here. In the winter of the deepest low

(1975/76), hares were found only in the three most preferred habitats, whereas in the two peak winters (1969/70 and 1978/79; and also during the increasing phase in 1977/78) observations were made in all the habitats available (Table). Rapid withdrawal from marginal habitats at times of declining populations has also been demonstrated in voles (TAMARIN 1978). WOLFF (1977) writes that "during the low phase of the hare cycle, hares are found only in the refuges, suboptimal habitats frequently having more food seasonally, but there being less cover and hares being more exposed to predation".

HÖRNFELDT (1978) found signs of a periodicity of 3–4 years in Swedish arctic hare populations on the basis of old catch records. The present data indicate one interval of four years between two lows, one interval of 4 or 5 years between two peaks and one interval of at least four years between two peaks (Table). Further studies are in progress to clarify the existence of fluctuations of 4 years or longer in this hare population.

KEITH and his associates (KEITH 1963, 1974; KEITH et al. 1977; KEITH and WINDBERG 1978) studied the 10-year cycle in the snowshoe hare population of central Alberta, Canada. KEITH and WINDBERG (1978) conclude their results to date as follows: "The cycle is repeatedly generated intrinsically through a hare-vegetation interaction (dominant herbivore vs. winter food supply) that triggers the population decline. This elevates the predator-hare ratio, thereby intensifying a second interaction that extends the period of decline and drives the hare population still lower. Interregional synchrony is caused basically by mild winters that moderate mortality in peak hare populations, and permit others that are lagging to attain peak densities. Such synchrony is reinforced by highly mobile predator populations". Predators are thus not the driving force (see also FINERTY 1980). This is also evidently true in the present study area, where the great predators played no role in the population dynamics of the hare population. Concerning the smaller carnivores and the predator-prey cycle, one would expect the predator cycle to follow the cycle in hare population. The figure shows that this was not the case. The local small predator populations were much more dependent on the small rodent populations for their nutrition (for further details, see PULLIAINEN 1981b).

Acknowledgements

The author wishes to express his sincere gratitude to the staff of the Värriö Subarctic Research Station for their technical assistance.

This paper constitutes Report No. 121 from the Värriö Subarctic Research Station of the University of Helsinki.

Zusammenfassung

*Zur Selektion des Habitats und zur Fluktuation des Bestandes von Schneehasen (*Lepus timidus*) auf einem subarktischen Fjäll im Waldlappland Finnlands*

Selektion des Habitats und Fluktuation des Bestandes von Schneehasen (*Lepus timidus*) wurden im Gebiet des Fjälles Värriö im östlichen Teil des finnischen Waldlapplands in den Wintern 1968/69 bis 1980/81 untersucht. Es ergab sich, daß der Hasenbestand zyklisch variierte. Die Dauer der Zyklen betrug mindestens vier Jahre. Bei geringer Bestandsdichte waren nur die bevorzugten Habitate (d. h. Mischwälder der niedrigen Gelände mit vorherrschendem Fichtenholz, in denen Birken und/oder Wacholder wuchsen) bewohnt, während in den Spitzenjahren Schneehasen auch in den weniger bevorzugten Habitaten, wie z. B. auf den windigen Abhängen der Fjällbirkenzone vorkamen. Bestandsverminderungen werden nicht durch Beutegreifer verursacht. In Jahren mit großer Bestandsdichte stieg die Bewegungsaktivität der Schneehasen während der Nahrungssuche im späten Winter erheblich an.

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